ELSEVIER

Journal of Cereal Science 38 (2003) 167–172

Journal of CEREAL SCIENCE

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Quantitative genetic analysis of acid detergent fibre content in barley grain

F. Han[a,1], S.E. Ullrich[a,*], I. Romagosa[b], J.A. Clancy[a], J.A. Froseth[c], D.M. Wesenberg[d]

[a]*Department of Crop and Soil Sciences, Washington State University, Pullman, WA 99164-6420, USA*
[b]*Universitat de Lleida-IRTA, 25196 Lleida, Spain*
[c]*Department of Animal Sciences, Washington State University, Pullman, WA 99164-6351, USA*
[d]*National Small Grains Germplasm Research Facility, USDA-ARS, Aberdeen, ID 83210, USA*

Received 30 October 2002; revised 3 February 2003; accepted 3 February 2003

Abstract

Acid detergent fibre (ADF) in cultivated barley (*Hordeum vulgare vulgare* L.) grain, a major indicator of digestibility, negatively affects feed quality, especially of non-ruminant livestock and poultry. Genetic studies of barley grain ADF content have been very limited. The objectives of this study were to map quantitative trait loci (QTLs) affecting ADF content to a molecular marker linkage map in barley, and to determine interactions among the QTLs identified. A population of 150 doubled haploid lines (DHLs) derived from a cross of 'Steptoe'/'Morex' was used for mapping. A total of five QTLs were identified; three with relatively large effects mapping adjacent to one another on chromosome 2H and one each on chromosomes 4H and 1H (5). The five QTLs explained 64.5% of total variation. Steptoe contributed high ADF alleles at all QTLs identified. In order to confirm that the three adjacent QTLs on chromosome 2H are distinct genetic units, three DHLs representing each QTL were selected for backcrossing to Morex. Analysis of F_2 ADF data from these three crosses showed that the three QTLs are distinct heritable genetic units. Additivity among the three major QTLs on chromosome 2H and the QTL on chromosome 1H (5) were observed.
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Keywords: Quantitative trait locus; Barley; Acid detergent fibre

1. Introduction

Barley, the fourth most produced cereal worldwide is a major feed grain crop. The energy value of barley is primarily affected by the levels of starch and less digestible fibre components such as acid detergent fibre (ADF), total (1 → 3,1 → 4)-β-glucans, arabinoxylans and other fibre components (Newman and Newman, 1992). ADF content is used as an indicator of digestibility in cereal grains, particularly for non-ruminants. In normal covered barley grain, ADF content typically ranges from about 4–8% (Ullrich et al., 1984) and is primarily found in the hull (palea and lemma) and pericarp. It consists mainly of cellulose and lignin, which are largely indigestible by non-ruminants including humans (Newman and Newman, 1992). The energy content of barley for poultry and pigs is decreased by high ADF levels (Miller et al., 1994). Breeding of barley with low fibre may result in grain with improved feeding quality. On the other hand, for human consumption a relatively high ADF content may be desirable, since cereal fibre is a generally recommended dietary component.

Compared to conventional plant breeding, molecular breeding procedures aided by molecular markers, promise to be more efficient and predictable (Paterson, 1998). Molecular breeding relies on the ability to associate traits of interest with molecular markers, and thus tag them in segregating populations. Most important agronomic and quality traits are quantitatively inherited, and therefore, controlled by a number of genes or quantitative trait loci (QTLs). Mapping of QTLs to chromosomes and identification of linked molecular markers are becoming routine in genetic study of crop plants, and the information is being

Abbreviations: ADF, acid detergent fibre; DHL, doubled haploid line; QTL, quantitative trait locus.

* Corresponding author. Tel.: +1-509-335-3475; fax: +1-509-335-8674.
E-mail address: ullrich@wsu.edu (S.E. Ullrich).
[1] Present address: Pioneer Hi-Bred Intl. Inc., 7200 NW 62nd Ave., Johnston, IA 50131, USA.

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doi:10.1016/S0733-5210(03)00020-1

used in breeding, as well. The objectives of this study were: (1) to map and confirm QTLs affecting ADF to a molecular marker linkage map in barley, and (2) to determine the interactions among the QTLs identified.

2. Materials and methods

2.1. Mapping population

A molecular marker linkage map (Kleinhofs et al., 1993) (current at http://barleygenomics.wsu.edu/) was developed by the North American Barley Genome Mapping Project from a 150 doubled haploid line (DHL) population derived from Steptoe/Morex F_1s, and used for mapping of ADF QTLs. Steptoe and Morex have relatively high and low ADF content, respectively. The 150 DHLs together with Steptoe and Morex were planted in the field at Pullman, WA in 1991 and 1992, at Aberdeen, ID in 1991, and at Tetonia, ID in 1992 under locally recommended management practices. Plots were arranged in a randomized complete block design with two replications. The harvested seed was used for ADF analyses.

2.2. ADF analyses

ADF was analysed by the method of Goering and Van Soest (1970). Briefly, barley flour was ground through a 0.5 mm screen on a UDY mill, and refluxed in digestion buffer for 1 h. from time of boiling. The residue was rinsed thoroughly and dried for 48 h at 50 °C in a forced air oven and the percentage residue was calculated. Duplicate analyses were done for each sample.

2.3. QTL mapping

QTL analyses were first conducted separately for each environment. As no genotype x environment crossover interaction (change in favourable allele type) was detected, we report QTLs based on multi-environment means. Analyses were performed using MAPMAKER/QTL (Lander et al., 1987; Lincoln et al., 1992). QTL effects were considered significant if they exceeded a LOD score of 2.4 ($p \approx 0.001$) (Lander and Botstein, 1989). The LOD peaks were considered to indicate the most likely position of QTL effects.

2.4. QTL verification

This was a follow-up experiment to the initial QTL mapping described above. Verification of certain QTLs was carried out by means of linked molecular markers to tag the alleles of each putative QTL. A QTL can be confirmed, if significant phenotypic variation in a segregating F_2 population from two genotypes differing only for this putative QTL is observed. To verify three major QTLs identified on chromosome 2H, DHLs with the appropriate alleles at putative QTLs were identified from the mapping population. That is, DHLs were selected that have a Steptoe allele (giving high ADF) for a given putative ADF QTL and Morex alleles (giving low ADF) for all other ADF QTLs (Table 1). Backrosses between high (a DHL) and low (Morex) ADF content parents were made in the greenhouse during the summer of 1995. These crosses were designed to have only one putative QTL segregating in any given cross. A total of 60 plants from each segregating F_2 population, together with parents, were planted in the field in the summer of 1997. The harvested seed were analysed for ADF content. Statistical contrasts were carried out between the high and low ADF parent and between each of them and the mean of their F_2 population. Statistical significance of these contrasts could be valid verification of a QTLs existence. Two alternative experimental error terms were used for these statistical comparisons: the intra-plant pooled error based on the two chemical determinations per genotype and on the plants within an F_2 population error term. Whereas the first one could underestimate the experimental error term, the second may overestimate it due to true genotypic effects within a population that would be associated with pure error. Statistical contrasts were carried out using SAS/STAT (Statistical Analysis System Institute, 1991).

2.5. QTL interaction

Interactions among identified QTLs were calculated based on standard analyses of variances of the ADF content

Table 1
Allelic constitution of three DHLs selected at the marker loci flanking the ADF QTLs identified

DHL	Chromosome 2H			Chromosome 4H	Chromosome 1H (5)
	Rbcs-ABG002 (ADF1)	Adh8-ABG019 (ADF2)	His3C–KsuF15 (ADF3)	WG622-ABG313 (ADF4)	ABA006-Hor2 (ADF5)
DH149	S	M	M	M	M
DH10	M	S	M	M	M
DH91	M	M	S	M	M

S-Steptoe allele; M-Morex allele.

data of different QTL genotype groups within the mapping population using SAS/STAT (Statistical Analysis System Institute, 1991).

3. Results and discussion

3.1. Phenotypic variation

The mean ADF content of the 150 DHL Steptoe/Morex mapping population over four environments was 7.53 ± 0.63%, with a range of 5.67–9.16%. The ADF contents of Steptoe and Morex were 8.94 and 6.39%, respectively. A normal frequency distribution of ADF for the DHL population was observed (Fig. 1).

3.2. QTLs identified for ADF content

A total of five QTLs were identified for ADF content (Table 2). Three QTLs were located on chromosome 2H with peak support intervals overlapping one another. The peak intervals of the three QTLs are *Rbcs*-ABG002 of 11.5 cM (hereafter referred to as 'ADF1'), *Adh8*-ABG019 of 6.6 cM ('ADF2'), and *His3C–KsuF15* of 11.9 cM ('ADF3'). These three putative QTLs, ADF1-3, had large effects as they explained 28.0, 28.4, and 24.7%, respectively, of the total variation in ADF content. There are QTLs of several potentially related traits that have been mapped with the Steptoe/Morex mapping population coincidently with these ADF QTLs. The QTL in the *Adh8*-ABG019 interval (ADF2) overlaps with a QTL for barley (1 → 3,1 → 4)-β-glucan content (Han et al., 1995) and one for starch content (Ullrich et al., 1996). All three traits

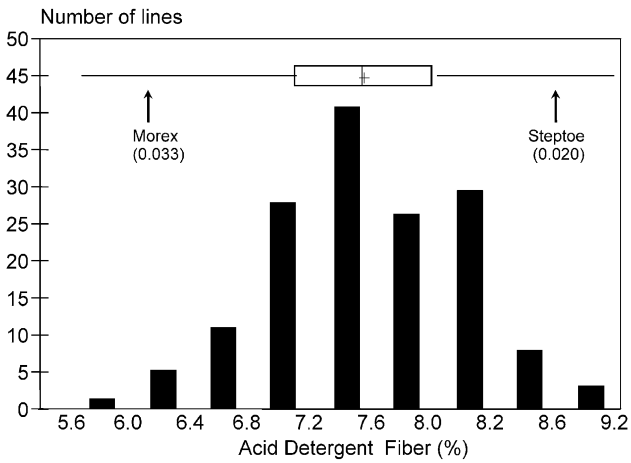

Fig. 1. Frequency distribution of barley grain ADF content in 150 DHL population derived from Steptoe/Morex. A box-plot is shown for the population. The horizontal line extends from the minimum to the maximum values, and the vertical line in the box shows the 1st, 2nd and 3rd quartile. The plus sign represents the arithmetic mean. The numbers in parentheses under each parent name indicates the proportion of DHLs with more extreme ADF values than the low (Morex) or high (Steptoe) ADF parent.

Table 2
QTL genotype difference in %ADF (Diff.) and variance (%var) explained where LOD score ≥2.4

Marker interval		% Recombination	ADF		
			Diff.	%Var	LOD
Chromosome 2H					
ABG313A	ABG703	7.9	0.43S	11.7	3.8
ABG703	Chs1B	11.0	0.49S	15.5	4.7
Chs1B	ABG008	7.2	0.56S	19.6	6.6
ABG008	Rbcs	4.6	0.60S	22.6	8.0
Rbcs	ABG002	11.5	**0.67S**	**28.0**	**9.1**
ABG002	ABG459	9.0	0.61S	23.2	7.8
ABG459	Pox	5.5	0.61S	23.5	7.9
Pox	Adh8	6.8	0.63S	24.7	8.5
Adh8	ABG019	11.7	**0.68S**	**28.4**	**8.8**
ABG019	**ABC162**	6.6	0.57S	19.8	6.6
ABC162	ABG014	8.3	0.60S	22.4	6.7
ABG014	His3C	10.3	0.61S	22.8	7.1
His3C	KsuF15	11.9	**0.64S**	**24.7**	**7.3**
KsuF15	Crg3A	22.1	0.53S	16.6	5.4
Crg3A	Gln2	16.4			
Gln2	ABC157	7.4			
ABC157	ABC165	7.4			
ABC165	Pcr1	7.5			
Pcr1	ABA005	8.6			
Chromosome 4H					
WG622	ABG313B	10.5	**0.39S**	**9.3**	**2.9**
ABG313B	CDO669	4.6			
CDO669	BCD402B	14.0			
BCD402B	TubA1	10.3			
TubA1	ABG003	4.8			
ABG003	**ABG484**	5.4			
ABG484	WG464	10.4			
WG464	ABG472	15.8			
ABG472	ABG500B	16.1			
ABG500B	ABG397	7.0			
ABG397	Bmy1	25.4			
Bmy1	KsuH11	3.3			
Chromosome 1H (5)					
AGA006	Hor2	2.5	**0.61S**	**23.6**	**8.1**
Hor2	Hor1	10.5	0.62S	24.1	7.7
Hor1	ABA004	6.6	0.46S	13.5	4.5
ABA004	CDO99	8.0	0.39S	9.0	2.9
CDO99	Ica1	11.2			
Ica1	ABG500A	7.9			
ABG500A	ABG494	9.9			
ABG494	**Glb1**	7.6			
Glb1	ABC160	8.8			
ABC160	ABG464	14.7			
ABG464	His3B	9.6			
His3B	iPgd2	16.6			
iPgd2	ABG702	12.6			
ABG702	ABA002	6.4			
ABA002	ABG373	8.3			
ABG373	ABG387A	5.3			

Values in bold type indicate LOD peaks. Adjacent values indicate the support interval. The letter suffix indicates the parent contributing the larger value allele, S-Steptoe; M-Morex. Marker interval in bold type indicates centromere location for each chromosome.

are related to carbohydrate content in barley grain, thus the overlapping QTLs might be due to pleiotropic effects. Heading date QTLs mapped coincidently with ADF1 and ADF3 (Hayes et al., 1993), which could impact grain filling, and thus, ADF content. Earlier heading is conferred by Steptoe alleles at both heading date QTLs. The QTL in the *Rbcs*-ABG002 interval (ADF1) might be related to the rubisco gene (*Rbcs*). Further dissecting of this region would be interesting.

The other two QTLs in the intervals of WG622-ABG313B (ADF4) on chromosome 4H, and AGA006-*Hor2* (ADF5) on chromosome 1H (5) account for 9.3 and 23.6% of the variation, respectively. Bowman and Blake (1996) also studying the Steptoe/Morex DHL population reported one QTL for ADF content near the centromere of chromosome 4H (near ABG484), which is apparently different from the one near the telomere of chromosome 4 reported here. The 5 QTLs identified in our study together explained 64.5% of the total variation. The large amount of variation explained by these QTLs could indicate high polymorphism of ADF content genes between the two parents. The alleles with the higher ADF value at all 5 QTLs are from Steptoe.

3.3. QTL verification

Since the three QTLs on chromosome 2H are adjacent, it was decided to verify their individual existences. As mentioned above, a QTL can be confirmed, when significant phenotypic variation for the trait can be observed if different alleles of the QTL are segregating. Therefore, three DHLs, each with a high ADF (Steptoe) allele for one of the QTLs identified on chromosome 2H and low ADF (Morex) at all other ADF QTLs (Table 1), were selected to backcross to Morex (with low ADF) to generate segregating populations. Sixty F_2 individuals from each population plus their parents were analysed for ADF content. Each population was set-up to segregate for only one of the five QTLs identified.

The three segregating populations had normal frequency distributions for ADF content instead of 1:2:1 ratios expected with Mendelian segregation (Fig. 2). This may be due to minor inaccuracies in the measurement of ADF content and/or environmental effects together with effects of the QTL under investigation. There also may be other undetected minor QTLs segregating with small effects. Statistical comparisons between the mean of the F_2 ADF crosses revealed that there are significant differences between progenies and parents for all three populations (bottom of Table 3). This result indicates that there is indeed a QTL segregating in each population, thus, these three adjacent QTLs (ADF1–3) appear to be distinct. The F_2 mean value and frequency distribution of ADF (Table 3, Fig. 2) also agree with the magnitude of the three QTLs identified by the original simple interval mapping. For example, the QTL in the *His3C–KsuF15* interval (i.e. ADF3) had the smallest effect among the three adjacent

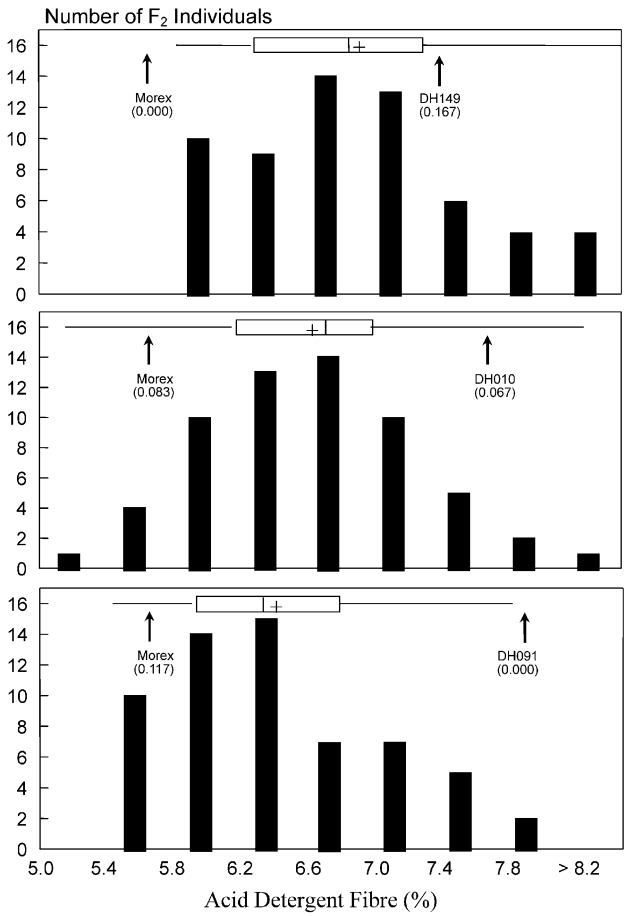

Fig. 2. Distribution of ADF in three F_2 populations from the crosses: Morex/DH149 (top); Morex/DH010 (middle); and Morex/DH091 (bottom). The high ADF Steptoe alleles for ADF1, 2, and 3 are present in each of these three DHL, respectively. A box-plot is shown for each segregating population. The horizontal line extends from the minimum to the maximum values, and the vertical line in the box shows the 1st, 2nd and 3rd quartile. The plus sign represents the arithmetic mean. The numbers in parentheses under each parent name indicates the proportion of F_2 individuals with more extreme ADF values than the low (Morex) or high (DH149, top; DH010, middle; DH091, bottom) ADF parent values.

QTLs, and the F_2 mean of ADF content in the cross Morex/DH91 representing this QTL was also the lowest.

3.4. QTL × QTL interaction

After confirming the existence of the three adjacent QTLs on chromosome 2H, their interactions with the other two QTLs were investigated with the original mapping population data. Each of three QTLs (ADF1, ADF2, ADF3) on chromosome 2H had significant additive interactions with ADF5 on chromosome 1H (5) and negative epistatic effects on ADF4 on chromosome 4H (Table 4). There were no significant ADF differences among genotypes SSMMSS, SSMMMM, MMSSSS, and MMSSMM (S and M represent Steptoe and Morex

Table 3
Average barley grain ADF values for four barley genotypes (DH149, DH10 and DH91 with high ADF and Morex with low ADF content) and three crosses and statistical contrasts between the parents and the F_2 means based on the pooled ANOVA error and based on the plant (cross) error

	DH149/Morex		DH10/Morex		DH91/Morex	
High ADF parent	7.52		7.79		7.91	
F_2 mean of 60 plants	6.96		6.69		6.46	
Morex	5.79		5.70		5.70	
CV (%)	10.34		10.46		10.22	
Statistical contrasts	Pooled error	Plant (cross) error	Pooled error	Plant (cross) error	Pooled error	Plant (cross) error
High ADF vs. Morex	0.0001[a]	0.0653[b]	0.0001	0.0345	0.0001	0.0251
High ADF vs. F_2	0.0001	0.4290	0.0001	0.1189	0.0001	0.0392
Morex vs. F_2	0.0001	0.0722	0.0001	0.1570	0.0001	0.2771
Midparent vs. F_2	0.0001	0.4770	0.4226	0.9187	0.0001	0.4895

[a] Statistical significance (probability) of the contrast between the high ADF parent, DH149 in this case, and Morex using the pooled error.
[b] Statistical significance (probability) of the contrast between DH149 and Morex using the plant (cross) error.

alleles, respectively; and within each group, the first pair of alleles represent ADF1 or ADF2 or ADF3, the second pair of alleles ADF5, and the third pair of alleles ADF4; Table 4). This indicates that the effect of ADF1 or ADF2 or ADF3 is equal to that of ADF5, and that ADF4 has no effect when ADF1 or ADF2 or ADF3 and ADF5 are present. Interactions between ADF4 and ADF5 were not significant (data not shown).

Five specific chromosome regions that affect ADF content in barley grain were identified from the six-row cross between Steptoe and Morex; three on chromosome 2H and one each on chromosomes 4H and 1H (5). The chromosome regions identified individually accounted for 9.3–28.4% of the ADF variability in the DHL mapping population, and together the five QTLs accounted for 64.5% of the variation. All five QTLs interact with each other in additive or epistatic manners. The information reported herein expands on that of the only other such study in barley (Bowman and Blake, 1996), which enhances our genetic understanding of this important cereal nutritional quality trait. This new information could impact the breeding of new barley cultivars with significantly elevated (for human food) or reduced (for animal feed) fibre contents depending on the objective. The data suggests that selection for low or high ADF content could be performed with the QTLs on chromosomes 2H and 1H (5). Since the three QTLs on chromosome 2H are linked, selection for these QTL could be done with relatively few markers. However, there are agronomic trait QTLs coincident with ADF1; grain yield (Steptoe allele increases yield), plant height (Morex allele increases plant height), and heading date (Morex allele delays

Table 4
Interactions between three adjacent QTLs on chromosome 2H and two other QTLs on chromosomes 4H and 1H (5)

Genotype			Least squares means of ADF (%)	Diff.[a]	Genotype			Least squares means of ADF (%)	Diff.[a]	Genotype			Least squares means of ADF (%)	Diff.[a]
ADF1	ADF5	ADF4			ADF2	ADF5	ADF4			ADF3	ADF5	ADF4		
SS	SS		8.00	A	SS	SS		8.11	A	SS	SS		7.98	A
SS	MM		7.53	B	SS	MM		7.49	B	SS	MM		7.42	B
MM	SS		7.51	B	MM	SS		7.44	B	MM	SS		7.48	B
MM	MM		6.83	C	MM	MM		6.82	C	MM	MM		6.97	C
SS		SS	7.88	A	SS		SS	7.93	A	SS		SS	7.86	A
SS		MM	7.65	AB	SS		MM	7.68	A	SS		MM	7.55	AB
MM		SS	7.25	BC	MM		SS	7.22	B	MM		SS	7.26	B
MM		MM	7.09	C	MM		MM	7.04	B	MM		MM	7.18	B
SS	SS	SS	8.10	A	SS	SS	SS	8.24	A	SS	SS	SS	8.09	A
SS	SS	MM	7.90	AB	SS	SS	MM	7.98	AB	SS	SS	MM	7.86	AB
SS	MM	SS	7.65	B	SS	MM	SS	7.61	BC	SS	MM	SS	7.62	BC
SS	MM	MM	7.40	BC	SS	MM	MM	7.37	CD	SS	MM	MM	7.23	CD
MM	SS	SS	7.58	BC	MM	SS	SS	7.46	CD	MM	SS	SS	7.45	BC
MM	SS	MM	7.45	BC	MM	SS	MM	7.42	CD	MM	SS	MM	7.50	BCD
MM	MM	SS	6.93	CD	MM	MM	SS	6.98	DE	MM	MM	SS	7.07	CD
MM	MM	MM	6.73	D	MM	MM	MM	6.66	E	MM	MM	MM	6.87	D

S-Steptoe allele, M-Morex allele.
[a] Least squares means followed by the same letter are not statistically different based on a t-test, $p \leq 0.05$.

heading) (Hayes et al., 1993). Therefore, replacing the Steptoe allele in the chromosome region of ADF1 with the Morex allele region could potentially decrease grain yield, increase plant height, and delay heading, while reducing ADF content. The other ADF QTLs are free of significant known negative trait associations.

Acknowledgements

The authors wish to thank A. Kleinhofs and F.J. Muehlbauer for their critical review of and helpful suggestions for this manuscript. Dep. of Crop and Soil Sciences Scientific Paper Number 080002-39, Agricultural Research Center, Washington State University, Pullman, WA, Project 1006.

References

Bowman, J., Blake, T.K., 1996. Barley feed quality for beef cattle. In: Scoles, G., Rossnagel, B. (Eds.), Proceedings of the V Int'l Oat Conf. & VII Int'l Barley Genet. Symp. Invited Papers, Univ. Saskatchewan Ext. Press, Saskatoon, Canada, pp. 82–90.

Goering, H.K., Van Soest, P.J., 1970. Forage fibre analysis (apparatus, reagents, procedures and some applications), Agricultural Handbook 379, ARS, USDA, Washington, DC.

Han, F., Ullrich, S.E., Chirat, S., Menteur, S., Jestin, L., Sarrafi, A., Hayes, P.M., Jones, B.L., Blake, T.K., Wesenberg, D.M., Kleinhofs, A., Kilian, A., 1995. Mapping of β-glucan content and β-glucanase activity loci in barley grain and malt. Theoretical and Applied Genetics 91, 921–927.

Hayes, P.M., Liu, B.H., Knapp, S.J., Chen, F., Jones, B., Blake, T., Franckowiak, J., Rasmusson, D., Sorrells, M., Ullrich, S.E., Wesenberg, D., Kleinhofs, A., 1993. Quantitative trait locus effects and environmental interaction in a sample of North American barley germ plasm. Theoretical and Applied Genetics 87, 392–401.

Kleinhofs, A., Kilian, A., Saghai Maroof, M.A., Biyashev, R.M., Hayes, P.M., Chen, F.Q., Lapita, N., Fenwich, A., Blake, T.K., Kanazin, V., Ananiev, E., Dahleen, L., Kudrna, D., Bollinger, J., Knapp, S.J., Liu, B., Sorrells, M., Heun, M., Franckowiak, J.D., Hoffman, D., Skadsen, R., Steffenson, B.J., 1993. A molecular, isoenzyme and morphological map of the barley (*Hordeum vulgare*) genome. Theoretical and Applied Genetics 86, 705–712.

Lander, E.S., Botstein, D., 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121, 185–199.

Lander, E.S., Green, P., Abrahamson, J., Barlow, A., Daly, M.J., Lincoln, S.E., Newburg, L., 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1, 174–181.

Lincoln, S.E., Daly, M., Lander, E.S., 1992. Mapping genes controlling quantitative traits with MAPMAKER/QTL 1.1, 2nd ed, Mass. Tech. Rep., Whitehead Inst. for Biomedical Research, Cambridge.

Miller, M.C., Froseth, J.A., Wyatt, C.L., Ullrich, S.E., 1994. Effect of starch type, total beta-glucans, and acid detergent fibre levels on the energy content of barley (*Hordeum vulgare* L.) for poultry and swine. Canadian Journal of Animal Science 74, 679–686.

Newman, C.W., Newman, R.K., 1992. Nutritional aspects of barley seed structure and composition. In: Shewry, P.R., (Ed.), Barley: Genetics, Biochemistry, Molecular Biology and Biotechnology, CAB International, Wallingford, UK, pp. 351–368.

Paterson, A.H., 1998. QTL mapping in DNA marker-assisted plant and animal improvement. In: Patterson, A.H., (Ed.), Molecular Dissection of Complex Traits, CRC Press LLC, New York, pp. 131–143.

Statistical Analysis System Institute, 1991. SAS user's guide. Statistics, Version 6.10, SAS Inst., Cary, NC.

Ullrich, S.E., Han, F., Froseth, J.A., Jones, B.L., Newman, C.W., Wesenberg, D.M., 1996. Mapping of loci that affect carbohydrate content in barley grain. In: Slinkard, A., Scoles, G., Rossnagel, B. (Eds.), Proceedings of the V Int'l Oat Conf & VII Int'l Barley Genet Symp. Poster Ses., vol. 1, Univ. of Saskatchewan Ext. Press, Saskatoon, Canada, pp. 141–143.

Ullrich, S.E., Honeyfield, D.C., Froseth, J.A., 1984. Variation in the composition of western grown barley. Proceedings of the Western Section of the American Society of Animal Science 35, 163–165.